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Extinction Rates in Archipelagoes: Implications for Populations in Fragmented Habitats

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Abstract: To study the effect of habitat fragmentation on population viability, I used extinction rates on islands in archipelagoes and estimated the relative probability of extinction per species on single large islands and sets of smaller islands with the same total area. Data on lizards, birds, and mammals on oceanic islands and mammals on mountaintops and in nature reserves yield similar results. Species are likely to go extinct on all the small islands before they go extinct on the single, large island. In the short term, the analysis indicates that extinction probabilities may be lower on a set of small islands. This is perhaps an artifact due to underestimation of extinction rates on small islands and/or the necessity of pooling species in a focal taxon to obtain estimates of extinction rates (which may obscure area thresholds and underestimate the slope and curvature of extinction rates as a function of area). Ultimately, cumulative extinction probabilities are higher for a set of small islands than for single large islands. Mean and median times to extinction tend to be shorter in the fragmented systems, in some cases much shorter. Thus, to minimize extinction rates in isolated habitat remnants and nature reserve systems, the degree of fragmentation should be minimized.

Las tasas de extinción en archipielagos: consecuencias para poblaciones en habitats fragmentados

Resumen: A fin de estudiar el efecto de la fragmentación del hábitat sobre la viabilidad poblacional, utilicé las tasas de extinción en islas y en archipiélagoes y estimé la probabilidad relativa de extinción por especie en islas grandes individuales y en conjuntos de islas pequeñas con la misma área total. Los datos sobre lagartos, aves y mamíferos que habitan islas oceánicas, mamíferos que viven en cimas de montañas y en reservas naturales, dan lugar a resultados similares. En términos generales, las especies tienen una mayor probabilidad de extinguirse primero en el conjunto de islas pequeñas y luego en la isla grande. El análisis indica que, a corto plazo, las probabilidades de extinción serían menores para un grupo de islas pequeñas. Esto quizás se deba a la subestimación de las tasas de extinción en islas pequeñas, y/o a la necesidad de agrupar especies dentro de un mismo taxón para obtener estimaciones de las tasas de extinción (esto podría ocultar los umbrales de área, y subestimar la pendiente y la curvatura de las tasas de extinción como función del área). En última instancia, las probabilidades acumulativas de extinción son mayores para el conjunto de islas pequeñas que para las islas individuales grandes. La media y mediana de los tiempos de extinción tienden a ser menores en los sistemas fragmentados, y en algunos casos, estos son mucho más cortos. Por lo tanto, para minimizar las tasas de extinción en los remanentes de hábitat aislados y en sistemas de reservas naturales, se debe minimizar el grado de fragmentación.

Introduction

Habitat fragmentation or population subdivision, either anthropogenic or natural patchiness, affects all species to varying degrees and has become a major concern in

conservation biology. Populations that we attempt to conserve are increasingly isolated in disjunct patches of habitat with little or no dispersal between them. Populations in isolated habitat fragments are vulnerable to extinction through demographic stochasticity, environmental stochasticity and catastrophes, loss of genetic heterozygosity and rare alleles, edge effects, and human disturbance (Janzen 1986; Goodman 1987; Shaffer

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1987; Burkey 1989; Burkey 1993a, 1993b). Demographic stochasticity in finite populations causes populations in a set of small remnant patches (fragmented system) to be more prone to extinction than populations in a large remnant patch (unfragmented/continuous system) with the same total area (Burkey 1989). Environmental stochasticity and random catastrophes, if they are sufficiently large and spatially uncorrelated enough, may be able to counteract the effect of demographic stochasticity and may potentially render populations in fragmented systems less vulnerable to extinction than populations in continuous systems (Goodman 1987; Burkey 1989). Whether they do or not is an empirical question, the answer to which depends on the organism in question, the relative spatial scale of the fragments, and the scale and spatial correlation of environmental variability. To determine the effect of habitat fragmentation on the viability of a focal species, we need to know the probability of extinction in patches of different sizes and the correlation structure of disturbances and population dynamics among patches. To obtain this information for vertebrate populations, we need experiments on prohibitively large spatial and temporal scales, with replicates of several patch sizes. Most prohibitive of these requirements is the long time required before extinctions are observed. It may be possible to use data from long-term and large-scale "natural experiments" on islands to study the effect of habitat fragmentation on species' risk of extinction over time.

It can be shown that the probability of extinction must decline with area faster than negative exponential for fragmentation to increase the probability of extinction (Burkey, in preparation). If the probability of extinction by any given time, P_e , declines as $e^{-k(\text{area})^x}$ (k is some positive constant) there is no effect of fragmentation for $x = 1$, but fragmentation increases the risk of extinction for $x > 1$ and decreases the risk of extinction for $x < 1$. Presently, there exists no theory that accurately predicts how species extinction rates change with area. While we have some vague ideas (from some very simple models) of how extinction probabilities decrease with area, we know virtually nothing about how extinction probabilities in natural populations change with the degree of habitat fragmentation (keeping area constant). The moments of the distribution of extinction times as a function of population size are known for some stochastic birth-death processes (Bailey 1964; Goel & Richter-Dyn 1974), but unfortunately these do not incorporate biologically reasonable forms of density dependence. If density dependence is incorporated in these simple models, it is usually in the form of some (reflecting) population ceiling. Without density dependence, there is no effect of fragmentation under demographic stochasticity (see Järvinen 1982; Burkey 1989);

realistic density dependence is essential to understanding the effects of habitat fragmentation on population viability. Stochastic birth-death processes with density dependence typically cannot be solved explicitly, and if anything is known about them usually only the mean time to extinction is reported (see Goodman 1987; Gabriel & Bürger 1992; Mangel & Tier 1993). Unfortunately, to calculate the time to extinction for different degrees of fragmentation, the complete distribution of extinction times (or the probability of extinction as a function of time) is required for populations in different sized areas. Consequently, these studies do not report the time to extinction of metapopulations or the probability of extinction as a function of the degree of habitat subdivision.

Species-area curves have been used extensively to discuss the relative merits of fragmented and unfragmented populations. This practice has given rise to a long-standing controversy, often referred to as the SLOSS debate (Single Large Or Several Small reserves). Several authors (see Abele & Connor 1979; Higgs & Usher 1980) have pointed out that the number of species in a set of small reserves depends not only on the slope of the species-area curves but also on the degree of species overlap between them, and that island biogeography theory (MacArthur & Wilson 1967) is equivocal on this issue. Many authors have pointed out that minimizing the risk of extinction for the species present in a reserve at establishment is the more pertinent goal in conservation efforts (see Diamond 1976a; Terborgh 1976; Whitcomb et al. 1976).

In this study extinction rates on islands of different sizes are used to estimate the relative risk of extinction for species in continuous and fragmented habitats (reserves). I amass data from the ecological literature on extinction rates as a function of area and use them to calibrate a model of extinction probabilities as a function of time and the degree of habitat fragmentation. I assume that populations in different habitat fragments have been completely isolated from one another. To incorporate dispersal between fragments, much more data would be needed—on density dependence in demographic rates and dispersal, spatial, and temporal correlation in population size between populations, and so forth—and population trajectories would have to be modeled explicitly (see Burkey 1989; Murphy & Noon 1992). My goal is to see how habitat fragmentation may affect the risk of extinction per species once fragments become completely isolated from one another. For this we need a more precise picture of how the probability of extinction in isolated habitat remnants changes with time and area for different organisms. As populations become increasingly isolated on remnant habitat islands in a sea of human development, they may not have any outside source populations (Terborgh 1976; Cole 1981). In populations where this has not yet happened,

it is important to understand how they will be affected by isolation and fragmentation (see Soulé et al. 1979). Furthermore, understanding the extreme of completely insularized reserves should help in understanding the effect of fragmentation in less isolated systems.

The data I have found that fulfill the requirements of isolation and contain the necessary information to estimate extinction rates have been gathered from oceanic as well as terrestrial "islands." I use the terms "fragmentation," "subdivided population," and "fragmented population" to refer to a system subdivided without any loss of area, as opposed to a continuous population or a single large population. That is, I compare the fate of populations on a single large island to that of populations distributed over a set of small islands of the same total area. In established usage, habitat fragmentation involves both loss of area and subdivision of remaining habitat, but because the effects of reducing area are relatively well understood I adopt the above usage—the better to understand the process of extinction in subdivided populations. The term "metapopulation" could favorably be applied to such a subdivided population. "Metapopulation," however, is often defined as "a set of local populations which interact via individuals moving among populations" (Hanski & Gilpin 1991), and I avoid the term because I generally assume that there is no dispersal between fragments. In reality, populations exhibit patchiness at multiple spatial scales, with dispersal between patches a continuum from complete isolation to panmixia. Consequently, every population can be regarded as a metapopulation to some extent, with some level of subdivision affecting its viability—perhaps at multiple scales. This complexity does not fundamentally alter the nature of the problem. I refer to habitat patches or fragments as islands or reserves and to sets of small habitat patches as archipelagoes.

Materials and Methods

Extinction Rates in Archipelagoes

No published field studies report extinction rates of a focal species across a range of island sizes. Some progress may be made if one is willing to substitute replicate species within a higher taxon for replicate populations within a species by pooling species within that taxon as

if they are equal with respect to extinction proneness. Still, very few studies report extinction rates of species on archipelagoes or contain the information needed to estimate extinction rates or extinction probabilities as a function of area. Many studies have been made of the number of species on islands, and species-area curves can be found for numerous archipelagoes. To glean extinction rates from these studies, however, one must know (1) the number of species at at least two different times; (2) the number of colonizations of new species, recolonizations, and speciation events *in situ*; and (3) the time between censuses (or since isolation). To be useful for my purposes, the number of islands and their range of sizes must be adequate, with sufficient representation at different spatial scales, and the amount of dispersal among islands and between islands and any mainland source must be negligible. The data sets that fulfill these requirements are listed in Table 1.

Small mammals have gone extinct at different rates on mountaintops of the Great Basin where they became isolated after the Pleistocene, when piñon-juniper woodlands were continuously distributed across the basin. "A mountain range was considered an island if it contained at least one peak higher than 10,000 feet [about 3120 m] and was isolated from all other highland areas by a valley at least five miles across [8 km] below an elevation of 7500 feet [2300 m]. This altitude corresponds approximately to the lower border of montane piñon-juniper woodland" (Brown 1971). Brown shows that the percent of faunal saturation is not significantly correlated with distance from the "mainland" (the Sierra Nevada or Rocky mountains). He also shows that the highest peak, nearest mainland, nearest island, and highest pass do not contribute significantly to a stepwise linear regression against the number of species inhabiting the islands, and he concludes that the rate of immigration of boreal mammals is effectively zero. Therefore, the assumption of independence within the archipelago is probably not violated, and estimates of extinction rates are not confounded by dispersal from outside. I assume that all mountaintops housed the full set of 13 mammalian species at the time of isolation 8000 years ago.

The Channel Islands off southern California lie at distances varying from 8 to 61 miles from the mainland. Diamond (1969) documented both the number of ex-

Table 1. Geographic location, taxon, time span, and reference for the data sets from which extinction rates as a function of area were extracted.

Location	Taxon	Time Span	Source
Montane Islands, Great Basin	boreal mammals	post-Pleistocene	Brown 1971
Channel Islands, California	land and freshwater birds	1917–1968	Diamond 1969
Greater Buka Island, Solomon Islands	land-bridge relict birds	post-Pleistocene	Diamond 1984
North American National Parks	mammals	1898–1983	Newmark 1987
Gulf of California Islands	lizards	post-Pleistocene	Richman et al. 1988

tinctions and the number of immigrations between 1917 and 1968, so extinction rates can be calculated from the number of extinctions among the species present in 1917. Turnover rates varied inversely with species diversities (which is correlated with island size), with no apparent effect of distance from the mainland or other islands.

The present-day Solomon Islands were joined into a single island, "Greater Bukida," in the Pleistocene. Extinction rates of land-bridge relict birds on the Solomon Islands were calculated from the reported number of relict species (out of 13) and the 10,000 years since isolation by rising sea-level. "These species are evidently unable ... or unwilling ... to cross water gaps" (Diamond 1984). I used data only from islands larger than one square kilometer because none of the 11 islands smaller than that had any land-bridge relict birds surviving. Three of the four smallest islands larger than one square kilometer also had no relict bird species left, and they were not used either. Because it was not known when they lost their last species, extinction rates could not be estimated (and because $\ln(0)$ is undefined [see equation 1] they could not be estimated even if the time had been known—without a linear approximation that also underestimates rates on small islands). Excluding the small islands, with the highest extinction rates, causes underestimation of the detrimental effects of habitat fragmentation on species viability.

Newmark (1987) reports the number of extinct species in the orders Lagomorpha, Carnivora, and Artiodactyla for 14 North American national parks located in the Rocky Mountains, Sierra Cascades, and Colorado Plateau. I calculated extinction rates from the number of mammalian species found historically, less the number of extinctions prior to park establishment, the number of post-establishment natural extinctions, and the time since park establishment. Newmark states that post-establishment loss of species is most probably attributable to "short-term insularization effects."

The islands off Baja, California, differ in time since isolation from the mainland from 6000 to 12,500 years. Wilcox (1978) showed that the number of extinctions per island increases with the time since the land-bridge was severed. The islands are far apart from each other but relatively close to the mainland. Thus, lizard populations on different islands are probably independent, but, on the post-Pleistocene time scale, recolonization from the mainland may cause an underestimation of extinction rates on small islands and consequently of the effect of fragmentation. Such dispersal has not been demonstrated, however, so I did not exclude these data. Following Richman et al. (1988), data from Tiburón and Cedros islands were not used, due to the impact of human settlement and of rats, goats, and burros on these islands.

Procedure

I assumed that all species within an archipelago can be treated as equal, so that the rate of extinction from a conglomerate of species in the community may be treated as representative of the extinction rate for a hypothetical species. The rate of extinction per species can then be estimated for each island as

$$\hat{\lambda} = \frac{\ln(S_0/S_t)}{t}, \quad (1)$$

where S_0 is the number of species present at the first census (at isolation or park establishment), S_t is the number of species present in the second census, and t is the number of years between censuses. The shape of the extinction rate as a function of area, $\lambda(A)$, determines the relative viability of subdivided and continuous populations. The absolute magnitudes of the extinction rates are not critical.

I regress $\hat{\lambda}$ against island area, A , and use the regression, $\lambda(A)$, to calculate the probability of extinction as a function of time and degree of fragmentation. For each data set, the regression was chosen that explained the largest proportion of the variance—that had the highest R^2 —among a linear, an exponential, or a logarithmic regression. Where this produced a better fit, areas were log-transformed following conversion to a metric unit in which all values were greater than unity.

Assuming that the extinction rate per species for a given island is constant through time or that it varies so that the cumulative extinction rate over the intercensus period is representative, extinction can be modeled as a Poisson process, and the probability of extinction per species by time t is

$$P_e = 1 - \exp[-\lambda(A)t]. \quad (2)$$

I assumed that the fate of a population (its probability of extinction) of any given species on an island is independent of the fate of conspecific populations on any other islands in the archipelago. Thus, the probability that all conspecific populations in a set of islands of a given size go extinct is the product of the extinction probability for each island. This assumption relies primarily on the lack of dispersal and recolonization from adjacent islands and on a relatively small spatial scale for any important disturbances. The probability that n populations on i islands of individual size A/n are all extinct by time t is

$$P_{e,n} = (1 - \exp[-\lambda(A/n)t])^n. \quad (3)$$

Because I could not make all possible comparisons of different degrees of fragmentation at all spatial scales, I compared the estimated extinction probability of the largest island in each data set with the estimated extinc-

tion probability of five areas, each one-fifth the size of the large island. This experimental design was chosen a priori.

Because the cumulative probability of extinction by time t for a system of n areas is as stated in equation 3, the probability density function of time to extinction is

$$p_{\epsilon,n} = \frac{dP_{\epsilon,n}}{dt} = \lambda(A/n)n \exp[-\lambda(A/n)t] (1 - \exp[-\lambda(A/n)t])^{n-1}, \quad (4)$$

and the mean time to extinction for a system of n islands of size A/n is

$$T_{\epsilon,n} = \int_0^{\infty} tp_{\epsilon,n} dt = \sum_{k=0}^{n-1} (-1)^{n-1+k} \binom{n-1}{k} \frac{n}{\lambda(A/n)(n-k)^2}. \quad (5)$$

I calculated $T_{\epsilon,n}$ for all n from one to twenty, and $A = A_L$, where A_L is the area of the largest island in each archipelago. This range was chosen a priori and keeps the area A_L/n within the range of the island sizes in the archipelagos from which $\lambda(A)$ was estimated.

Setting $P_{\epsilon,n} = 0.5$ in equation 3 and solving for t , the median time to extinction is

$$M_{\epsilon,n} = \frac{-\ln(1 - \sqrt{0.5})}{\lambda(A/n)}. \quad (6)$$

Other percentiles can be obtained by substituting the appropriate proportion for 0.5. They can also be read directly from figures of $P_{\epsilon,n}$ versus t .

Because extinction rates were estimated from a common pool of all species in the focal taxon in the island, I interpreted the extinction probabilities and extinction times estimated as applying to some hypothetical average species. This washes out individual species thresholds in area requirements and means that quantitative information is not accurate for any particular species. Median times to extinction are best interpreted as the expected time til 50% of the species on the island have gone extinct. Extinction-prone species will have much lower persistence and much higher rates of extinction than the hypothetical "Chimera" and will probably be much more negatively affected by habitat fragmentation. For this and other reasons discussed below, the present analysis yields conservative estimates of fragmentation effects.

Results

Extinction rates per species decreases with increasing island area (Fig. 1). Simple, monotonically decreasing, linear, exponential, or logarithmic regressions against

area explain 52–96% of the variation in extinction rates per species. These relationships are the $\hat{\lambda}(A)$ used to estimate the effect of population subdivision on the risk of extinction.

The mean time to extinction for all the focal species on an island of area A can be estimated from the present data sets. If extinction is a Poisson process, the mean time to extinction is $1/\lambda(A)$. Estimated mean time to extinction for single-island populations is shown in Figure 2. All sets indicate that the mean time to extinction increases with area. The exact pattern in which T_{ϵ} increases with area appears to vary among taxa, geographic locations, and spatial scales.

Figure 3 shows the cumulative probability of extinction as a function of time for a single island (equal to the largest island in the respective archipelago) and for a set of five small islands (each one-fifth the area of the large island). The estimated median time to extinction was shorter in a set of five small islands than in a single large island for all data sets except that for the study by Richman et al. (lizards islands in the Gulf of California), where it was marginally longer.

Figure 4 shows the estimated mean time to extinction for an area divided into $n = 1$ to 20 fragments, based on equation 5. The mean time to extinction was shorter in a set of five small islands than in a single large island for all data sets. In all cases, the difference was large. In all data sets, an unfragmented large area had greater mean time to extinction than sets of any $n \leq 20$. Because extinction times in Figures 2 and 4 in effect are the mean times to extinction for all species on the islands, the relevant temporal scales for the most extinction-prone species (which we are most concerned about) are much shorter than the scales of the ordinate axes may suggest.

The best-fit regression for the mammals of U.S. and Canadian national parks went into negative extinction rates at approximately $12,000 \text{ km}^2$, which is smaller than the largest reserve system at $20,736 \text{ km}^2$ (see Fig. 1). Consequently, with this data set the area of the second largest park ($10,328 \text{ km}^2$) was used as the basis for calculations in Figure 4 using the regression shown in Figure 1; in Figure 3 the calculations were based on the area of the largest park, using an exponential function ($\hat{\lambda}(A) = 0.0025 * 10^{-0.00019A}$, $R^2 = 0.50$) that does not return negative extinction rates. The two treatments gave qualitatively similar results.

The mean time to extinction is greater than the median because distributions of times to extinction are bounded at zero but not above. The difference is greatest for single large islands because their curves for P_{ϵ} as a function of time are less steep (the exponents—in equation 3—are one rather than some larger integer). It is the nature of equation 3 that, for n greater than one, the cumulative probability of extinction is

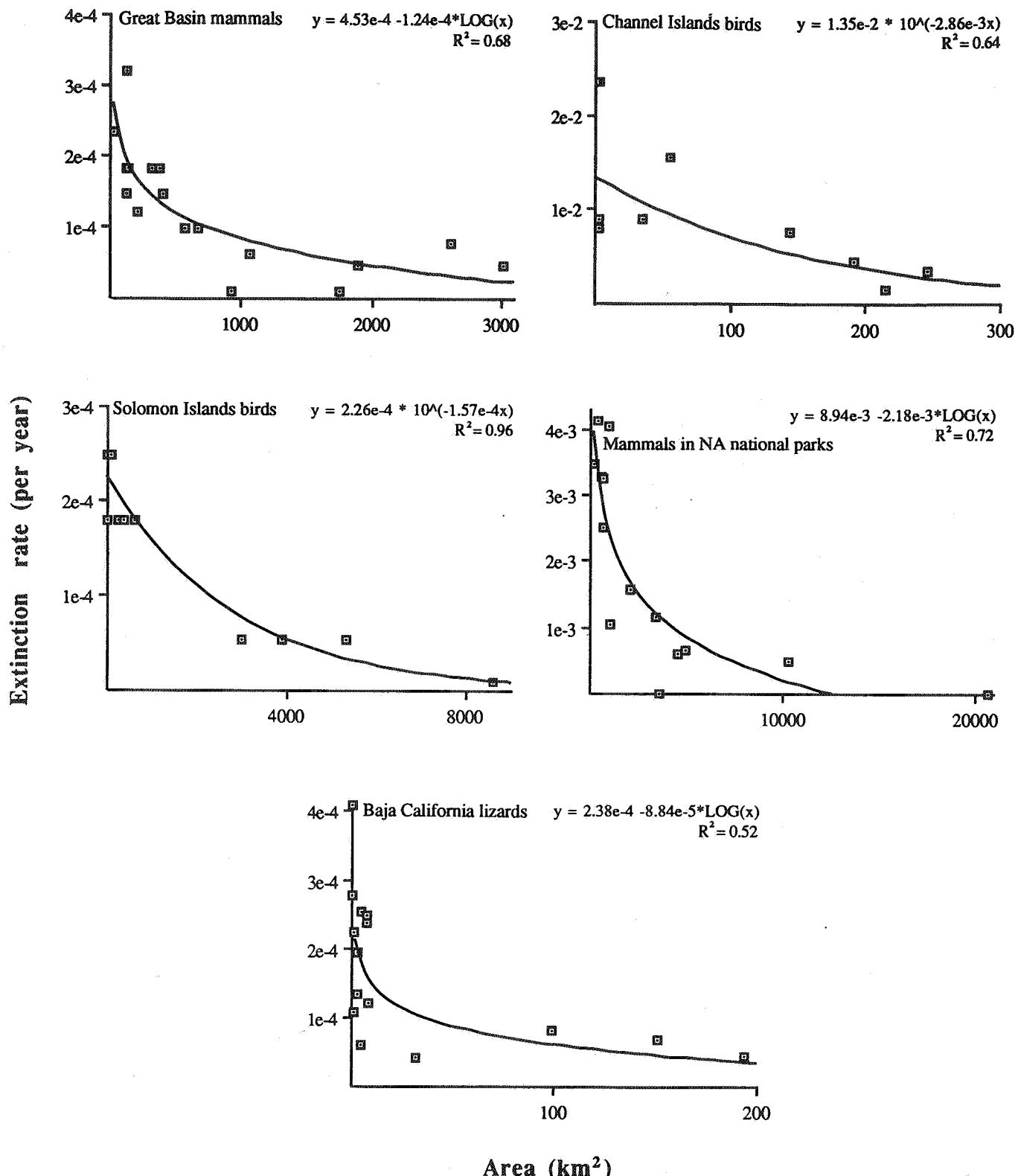


Figure 1. Simple regressions of extinction rates per species against area for mammals on mountaintops in the Great Basin (Brown 1971), land and freshwater birds on the Channel Islands of California (Diamond 1969), land-bridge relict birds on the Solomon Islands (Diamond 1984), mammals in U.S. and Canadian national parks (Newmark 1987), and lizards on islands in the Gulf of California (Richman et al. 1988). In each case the simple linear, exponential, or logarithmic function that explained the greatest portion of the variation in the data (with or without log-transforming the island area) was selected as the estimate of the area dependent extinction rate, $\hat{\lambda}(A)$. $\hat{\lambda}(A)$ is later used to calculate the cumulative probability of extinction as a function of time and degree of fragmentation ($P_{\epsilon,n}$; Fig. 3) and the mean time to extinction as a function of the degree of fragmentation ($T_{\epsilon,n}$; Fig. 4).

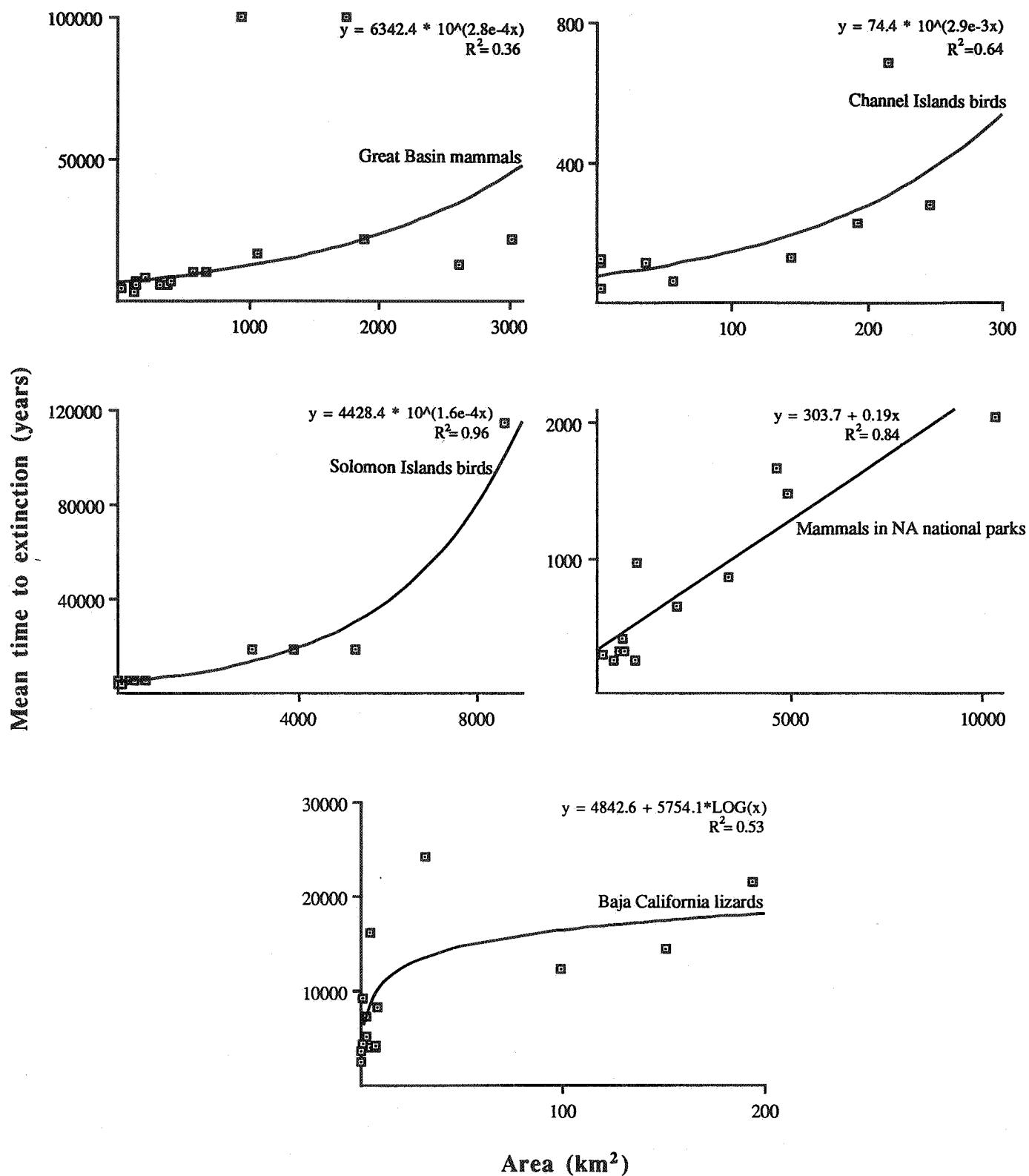


Figure 2. Mean time to extinction, $T_{\epsilon,1} = 1/\hat{\lambda}(A)$, as a function of area for a single island, for mammals on mountaintops in the Great Basin (Brown 1971), land and freshwater birds on the Channel Islands of California (Diamond 1969), land-bridge relict birds on the Solomon Islands (Diamond 1984), mammals in U.S. and Canadian national parks (Newmark 1987), and lizards on islands in the Gulf of California (Richman et al. 1988). Assuming that population size scales linearly with area, the mean time to extinction should increase exponentially with area if extinction is caused primarily by demographic stochasticity, linearly if environmental stochasticity is responsible, and hyperbolically if catastrophic events are responsible. The regressions are not shown for quantitative reasons, but merely to guide the eye (but see figures in Shaffer 1987 and Lande 1993).

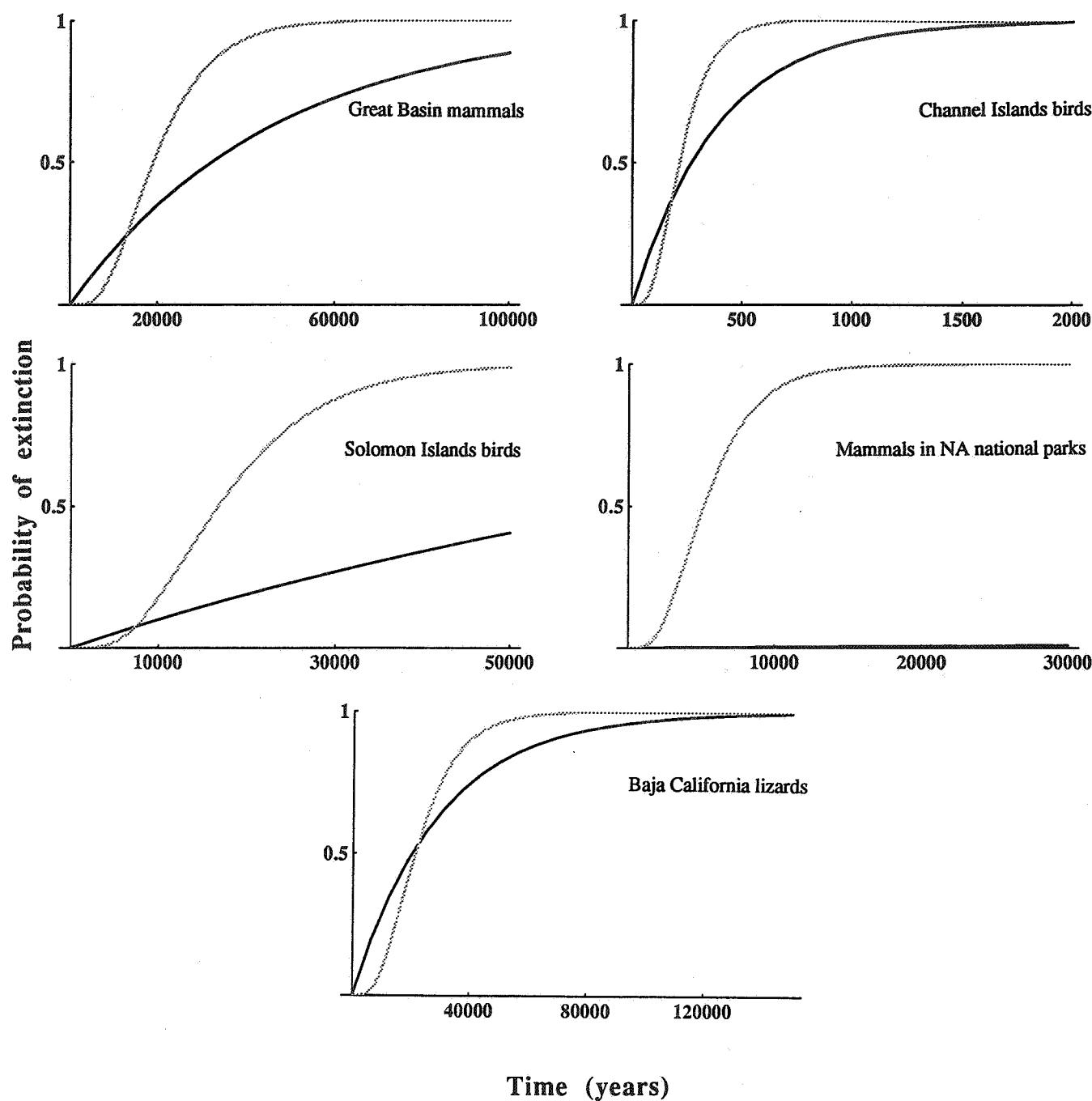


Figure 3. The cumulative probability of extinction $P_{e,n}$ (from equation 3) as a function of time (in years) for a single large island (black line) and for five small islands, each one-fifth the size of the single large island (grey line). These probabilities are obtained by putting $\hat{\lambda}(A)$ from each data set (from Fig. 1) into equation 3, with $n = 1$ and $n = 5$ and $A = A_L$ where A_L is area of the largest island in each data set. For the mammals of North American national parks, the regression $\hat{\lambda}(A) = 0.0025 * 10^{-0.00019A}$ ($R^2 = 0.50$) was used, and calculations were based on the area of the largest park ($20,736 \text{ km}^2$; see main text). The positioning of graphs corresponds to the same in Figures 1 and 2.

relatively flat initially and then steeper the greater the value of n . For greater values of n , the initial flat region is longer. For $n = 1$ there is no initial flat region—the probability of extinction with respect to time is not

sigmoidal in the unfragmented case. In all data sets, the estimated probability of extinction in fragmented systems was lower in the short term but greater in the long term than in less fragmented systems.

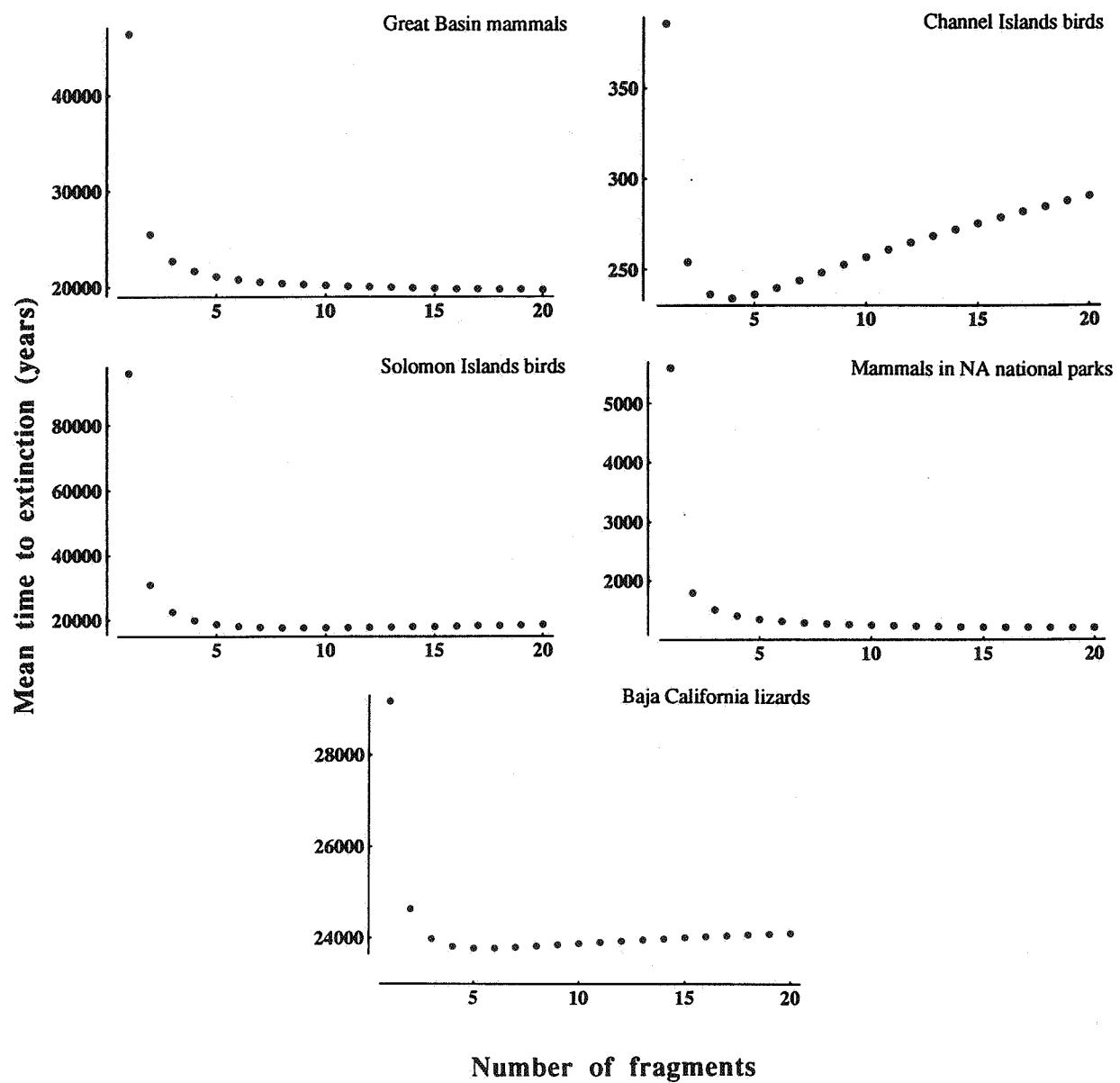


Figure 4. The mean time to extinction ($T_{e,n}$, from equation 5) for an area equal to the largest island in the respective data sets, as divided into different numbers of fragments. Note the common flattening out at high n and that some even increase again (slightly) after a strong initial decline. In the case of mammals of North American national parks, $T_{e,n}$ was calculated based on the area of the second largest park ($10,328 \text{ km}^2$) using the regression shown in Figure 1 (see main text). The positioning of graphs corresponds to the same in Figures 1, 2, and 3.

Discussion

My results support the assumption of MacArthur and Wilson (1967) that extinction rates decrease with increasing island area (Fig. 1). Consequently, the mean time to extinction increases with island area (Fig. 2). Several models predict that, where demographic stochasticity is the causal agent in extinction, the mean time to extinction should increase exponentially with area (see MacArthur & Wilson 1967; Goodman 1987). If

environmental stochasticity or catastrophes are responsible, the mean time to extinction should increase less rapidly than exponentially with area (linearly or hyperbolically, respectively [Shaffer 1987]). Habitat fragmentation is most likely to increase the probability of extinction if the mean time to extinction increases exponentially with area, but the complete distribution of extinction times is needed to determine the outcome in any given case. While some of the mean extinction times in Figure 2 seem to increase exponentially, some

linearly and some hyperbolically with area, I make no claims about these shapes or their relevance here.

All five data sets (Fig. 4) yielded longer mean persistence times for unfragmented populations than for fragmented populations ($n = 1$ versus $n = 2-20$). Four of five data sets yielded longer median persistence times for a single large population than for one fragmented into five subpopulations (Fig. 3). The one data set in which a continuous population had a shorter estimated median persistence time than a set of five subpopulations (data of Richman et al. for lizards on islands of Baja California) is the case in which the difference between medians had the smallest magnitude. This negative effect of fragmentation on persistence time matches the strong effect of fragmentation observed in computer simulations of populations under demographic stochasticity (Burkey 1989; 1995a) and in numerical solutions of density-dependent stochastic birth-death processes (Burkey 1995a).

Temporal and Spatial-Scale Dependence

The probability of overall extinction in a set of n fragments is $P_e = (1 - \exp(-\lambda(A/n)t))^n$, which is sigmoidal with t for $n > 1$ but hyperbolic for $n = 1$ (see Fig. 3). Thus, whenever the extinction probability in the single large reserve is low (large spatial scale and/or short time scale relative to the life-history of the organisms in question), the extinction probability in an archipelago of n smaller islands is the n^{th} power of some relatively small number (unless $\lambda(A)$ is very steep), which will be very small if n is large. This strictly numerical forcing is powerful enough to cause the temporal-scale dependence observed in Figure 3. As long as the risk of extinction is low, a subdivided population is apparently favored; continuous populations become favored as the risk of extinction increases. Without incorporating biological mechanisms that this procedure ignores, we may expect fragmentation to reduce extinction probabilities in the short term and to increase them in the long term, relative to the relevant spatial scale for the organism. Hence, a short-term experiment may be likely to indicate that fragmented populations survive longer than unfragmented populations. The probability of extinction must decline with area faster than negative exponential for fragmentation to increase the probability of extinction at any given time scale (Burkey 1995a).

It is possible that whether or not a single large reserve is a better safeguard against extinction than several reserves of equivalent size depends entirely upon the relative spatial and temporal scales. Certainly, if the temporal scale is too small relative to the spatial scale of a study, no populations will go extinct regardless of the degree of fragmentation, and no differences will be detected. Similarly, if the temporal scale is too large, all populations will be extinct and no treatment effect can

be detected. I believe, however, that the apparent short-term advantage to subdivided populations observed (Fig. 3) is primarily an artifact of the procedure used, especially the pooling of species in higher taxa in order to obtain estimates of extinction rates. There is no evidence of such scale dependence in demographic stochasticity models (Burkey 1989; 1995a), nor in the single published experiment (Forney & Gilpin 1989, on laboratory populations of *Drosophila melanogaster*) or in laboratory communities of bacteria and protozoa (Burkey 1995a).

When population trajectories of a focal species are modeled explicitly, with demographic stochasticity and density dependence, the short-term advantage to fragmented systems is not observed. If the observed scale dependence were due to the tradeoff between demographic stochasticity (favoring single large islands) and spatially uncorrelated environmental stochasticity (favoring several small islands), one would think that the observed relationship would be reversed (favoring a single large island in the short term and several small islands in the long term [see Goodman 1987]). The slopes and curvatures of P_e as a function of area are most likely underestimated because small islands have more extinctions and therefore more extinctions that are missed by the observer. The true functions, $\lambda(A)$, are steeper than the estimates presented, here and would favor single large islands more strongly than my results suggest. In addition, individual species probably have steeper (more curved) extinction probabilities against area than a conglomerate of pooled species with different area requirements and population densities (Diamond 1978, 1984; Terborgh & Winter 1980; see Fig. 5). Hence, I would not trust the apparent short-term advantage to fragmented systems until it has been corroborated in other analyses.

Extinction rates for lizards are an order of magnitude lower than for birds on Neotropical islands and mammals on western North American mountaintops (Diamond 1984). This may cause the apparent short-term advantage to fragmented systems to last even longer in the analysis based on the lizard data (see Fig. 3). That may help to explain why the lizards on islands in the Gulf of California are the only group in which the estimated median time to extinction is longer for a set of five fragments than for a single large island. Together with that for the birds of the Channel Islands, it is also the data set most likely to have underestimated extinction rates due to dispersal from the mainland. It is reasonable to expect that the species that are least vulnerable to extinction will be the least affected by fragmentation. Furthermore, Richman et al. (1988) used a species-area curve for the present-day mainland to estimate the number of species present on the islands at the time of isolation, based on their current area. These estimates are likely to be low because each island prob-

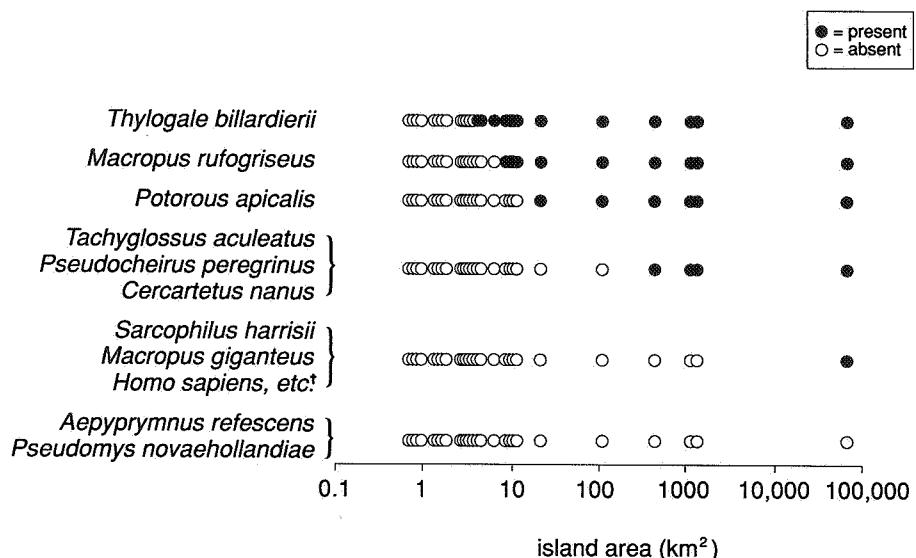


Figure 5. Distribution of flightless mammals on islands of the Bass Strait as a function of island area (adapted from Diamond 1984). This pattern was produced by differential extinction following isolation from the Australian mainland in the late Pleistocene (Diamond 1984). There is fossil evidence for the past existence of almost all modern Tasmanian species on smaller islands where they are now absent (see Hope 1973). The two species on the bottom line have disappeared from all the islands and now persist only on the Australian mainland. †The group second from the bottom also includes *Dasyurus viverrinus* (quoll), *Thylacinus cynocephalus* (Tasmanian "wolf" present until at least 1930), *Mastacomys fuscus* (broad-toothed rat) and *Pseudomys higginsi* (long-tailed rat), *Parameles gunnii* (brown bandicoot), *Betogia gaimardi* (eastern bettong), and *Anthechinus swainsonii* (broad-footed marsupial "mouse"), which all survived only on the largest island, Tasmania (data from Hope 1973).

ably sampled species from large tracts of land as animals moved to higher ground in response to the rising sea level. Consequently, the number of lizards that have gone extinct on the smaller islands may be greatly underestimated—another reason why the detrimental effect of habitat fragmentation may be underestimated, particularly for the lizards.

Quinn and Hastings (1987) estimated extinction rates in archipelagoes to study extinction in subdivided habitats, but they used a different method and different data sets than I did—and they reached a different conclusion. They assumed that T_e for a single population increases as the natural log of the population size—which may or may not be true (Fig. 2; see also Goodman 1987)—to obtain an approximate expression for T_e for a set of n reserves; they used two data sets with too few points for my regression-based method ($n = 6$); they used data from Nilsson and Nilsson (1982) that were taken on a prohibitively small spatial scale (at which there was no relationship between extinction rate and area, and the only correlate of extinction risk was the proportion of populations consisting of a single individual); and they used data from Diamond (1984) for birds on Northern European islands and from Väisänen and Järvinen (1977) on wading birds on the Krunnit islands in the Gulf of Bothnia, which are too panmictic to yield good estimates of extinction rates. Many of the species in

Diamond's data, and all of Väisänen and Järvinen's species, are migratory birds with extreme dispersal abilities. In the data from Finland there was frequent recolonization by extinct species. Quinn and Hastings (1987) unfortunately used a column of "turnover," compiled by Väisänen and Järvinen (1977), directly, which are not per-species extinction rates (they are turnover rates, unweighted averages and not per species). Their comparison of population persistence in fragmented and unfragmented systems was based exclusively on mean times to extinction, which, as they pointed out, was a bad metric for their purpose. They concluded that there is "no uniform tendency for the hypothetical expected time to extinction either to increase or decrease with size versus number of islands." I believe that the data presented here are more appropriate for such a test, that my procedure is more powerful, and that it is a useful way to extract what little information is available to study the effects of fragmentation on extinction risk.

Even in the data sets presented here, using my procedure, the relationship between mean time to extinction for fragmented and unfragmented systems is different at spatial scales other than the one chosen (a priori) for Figure 4. For the mammals on Great Basin mountain-tops (Brown 1971), for instance, dividing a 2000-km² area in fifths increases the risk of extinction, but dividing a 200-km² area in fifths appears to reduce the risk of

extinction. For birds of the Solomon Islands (Diamond 1984), dividing an island smaller than about 2900 km² into fifths reduces the extinction risk per species, but fragmentation of islands greater than 2900 km² increases extinction risk. This scale dependence is somewhat counterintuitive and may also be an artifact of the procedure. Although the fits were uniformly good, some $\hat{\lambda}(A)$ functions (Fig. 1) seemed not to be steep enough at small spatial scales—in other words, the type of functions used were not sufficiently curved. If the regressions for extinction rate versus area were steeper, both the potential temporal and spatial-scale dependences would be less pronounced. If the spatial scale dependence is not an artifact, it may be related to the spatial scale and temporal scale of disturbance events. More work is required to develop mechanistic models that yield realistic functions for $\hat{\lambda}(A)$ and to gather the data needed to calibrate the present model with extinction rates for individual species.

The same potential artifact may be responsible for the flattening out of the mean time to extinction as a function of n , seen in Figure 4. As n increases it takes longer and longer for P_e as a function of time to start its incline, and the incline gets ever steeper— P_e becomes increasingly like a step function (see equation 3). Variance in the time to extinction is reduced. For extreme values of n , the incline may be postponed long enough that the mean time to extinction increases. Biological mechanisms that the present procedure does not capture, however, probably vastly increases λ at such extreme degrees of fragmentation, so that this increase does not actually occur. Hence it would probably be a better test to take a large range of areas and divide them all in half or fifths than to take one area and divide it into as much as twentieths. The increase in mean time to extinction from intermediate to high degrees of fragmentation, seen in some data sets (Fig. 4—land and freshwater birds on the Channel islands and lizards on Baja California islands), is associated with the least difference in median extinction times (Fig. 3). They are also the data sets most likely to lead to underestimation of extinction rates on small islands, due to possible dispersal from the mainland. The same upturn in T_e for large n occurred when the spatial scale for the switch in the aforementioned spatial-scale dependence was approached. When the switch occurs, it comes first to the most fragmented systems.

One reason why Quinn and Hastings (1987) found no relationship between T_e and n is that they considered values of n as high as 10^6 . Even for values around 20, the cumulative probability of extinction as a function of time is so highly curved that it resembles a step function, and the location of the step approaches a limit. Biological effects probably render such high levels of fragmentation inappropriate for their method and mine. Reserves less than $1/20$ the size of a single large reserve

will likely house different species than the large reserve does, and other processes will be important. Such biological differences are not captured by my approach or theirs. Therefore, I caution against the premature interpretation that the flat sections of graphs in Figure 4 indicate that some degree of fragmentation may have little effect on particular spatial scales. To gain confidence in the results and to alleviate this fear of artifacts, I hope that more data sets become available in which the effect of habitat fragmentation can be explored further using the present procedure and refinements of it—preferably for individual focal species. In retrospect, the a priori decision to compare a single large island with five small islands may have been suboptimal, but to do otherwise with knowledge of the data would be data dredging and would invalidate the test.

If the temporal scale dependence observed proves not to be an artifact, proposed definitions of viability may have some unfortunate consequences. These definitions define viability in terms of some (low) probability of extinction within some arbitrary (short) time period and tend to take the form "95% chance of persistence for 100 years" or "99% chance of persistence for 1000 years" (Shaffer 1981, 1987; Soulé 1987). These definitions might lead us to opt for a conservation strategy—multiple small reserves—that may minimize the probability of extinction in the short term while maximizing it in the long term (Fig. 3).

Discussion of the Procedure and Its Assumptions

The conclusions of this study rest on the fit of simple equations to data. The procedure chosen was to fit linear, exponential, or logarithmic functions of area and of the logarithm of area and always to choose the regression with the highest R^2 value. This procedure gives a battery of functions with much flexibility that can be trusted to decrease monotonically with area. Some obvious alternatives are functions such as $\lambda(A) = \exp[-cA^x]$, where x is some integer, or $\lambda(A) = \exp[-c_0 - c_1A - c_2A^2 - \dots - c_nA^n]$. These were rejected because the first trades off steepness for small A against steepness for large A , and the second does not necessarily change monotonically with area.

Some of my assumptions are demonstrably false, notably the assumption that all species on the islands in question have equivalent extinction rates (see Diamond 1976a, 1976b; Terborgh 1976; Diamond 1984). That assumption may be expressed less stringently by assuming that species can be pooled to yield a meaningful composite estimate of extinction rates, or of a representative shape for extinction rates as a function of area. The procedure underestimates the rate of extinction and the effect of fragmentation on focal species because the extinction rates per species were estimated from a mean of many species, both extinction prone and ex-

tinction resistant. The species that do go extinct tend to be the same on all islands (Diamond 1976, 1984; Terborgh & Winter 1980; Patterson 1987; Fig. 5). Extinction-prone species are the ones conservation biologists are particularly concerned with (Diamond 1976; Terborgh 1976). These will go extinct faster and be more affected by fragmentation than my analysis suggests.

For some species, incidence functions with steep thresholds have been identified (Diamond 1976b; Diamond & Marshall 1977; Diamond 1978), indicating particular spatial scales at which fragmentation will have drastic and detrimental consequences for the population. The composite extinction functions resulting from my regressions may be less steep than such functions derived from individual species. It seems that the regressions used were not steep enough or curved enough, especially at small spatial scales, to capture the variation in the extinction rate data (see Fig. 1). Consequently, the detrimental effects of fragmentation were probably underestimated in this study. It is also possible that extinctions are more frequent immediately after isolation, tapering off with time. This would affect small islands more, once again contributing to an underestimation of the detrimental effects of habitat fragmentation.

Because the procedure rests heavily on the assumption of independence between islands, and representative estimation of extinction rates across islands of different sizes, the procedure can be used only where dispersal is negligible—both between islands and between islands and any mainland source. The studies reported here are of taxa and sites with quite limited dispersal for which that is probably true, or very nearly so. Several of the authors report that dispersal or distance to adjacent islands and mainland source pools had no detectable effect on extinction rates. Hence, the extinction of a conspecific population on one island should have no significant effect on the extinction probability on adjacent islands. I have excluded data from taxa with great dispersal abilities, such as migratory birds, or data where extinction rates were found to be correlated with distance from a mainland source. If there were dispersal from an outside source, extinctions would be missed between censuses, or they would not occur when they might have. Small islands have more extinctions than large islands, so extinction rates would be disproportionately underestimated on small islands. Populations that we attempt to conserve now and in the future may not have any mainland source populations, and the relevance of results from archipelagoes with outside recolonization may be reduced (Terborgh 1976; Cole 1981).

Large-scale disturbances and spatially correlated environmental variability (stochasticity) may also introduce dependence between habitat fragments. If extinctions in different fragments are partially correlated due

to large-scale environmental correlation, and not independent as my analysis assumes, persistence in fragmented systems will be further reduced.

Supplementary Data and Analysis

The multiple assumptions required to extract information from existing data are certainly cause for caution against over-interpretation of this study. Unfortunately, this is perhaps the best we can do in terms of field data—and new data on the effects of habitat fragmentation on extinction probabilities on appropriate spatial and temporal scales will be slow in coming. I hope, therefore, that more data on extinction rates as a function of area can be extracted from the literature—ideally for individual species. It may prove possible to extract this data from incidence functions of individual species. If it can be assumed that individual species were at some point present in all the islands of a particular set, it may be useful to use a binomial maximum likelihood estimator to fit a logistic regression to these data (binomial—presence or absence) against area. From that we may be able to derive estimates of extinction rates against area, which can be used to calculate probabilities of extinction as a function of time, area, and degree of fragmentation. Replication of islands with similar areas is the limiting factor in this endeavor.

A figure from Diamond (1984, based on data from 1973) does not yield an incidence function, but it shows so clearly the existence of steep thresholds in the persistence of populations with island area that it is reproduced here (Fig. 5). The species are perfectly nested (Patterson 1987): each species is absent on all islands smaller than a critical size and present on all islands larger than that size. For instance, the rat-kangaroo *A. rufescens* and the mouse *P. novaehollandiae* disappeared from all islands and survives only on the Australian mainland. The marsupial “cat,” *Dasyurus viverrinus*, *H. sapiens*, and nine other species survived on Tasmania and no other island. Carnivores are more susceptible to habitat fragmentation than herbivores, large carnivores more than small carnivores, and habitat specialists more than generalists (Diamond 1984). The steep threshold in area requirements for the different species suggests a strong negative effect of fragmentation, which is not captured by the technique used in the present study. This is perhaps the clearest indication we have of how habitat fragmentation and habitat loss may affect natural communities.

We can approximate the probability of extinction for different degrees of habitat fragmentation from some existing models. The mean time to extinction for a single population, assuming a Poisson distribution is $T_e = 1/\lambda$. In the stochastic birth-death process studied by Gabriel and Bürger (1992), the time to extinction is approximately geometrically distributed (it cannot be ex-

actly like any standard distribution because the earliest time at which extinction can occur is after N_0 time steps, where N_0 is the initial population size). For the geometric distribution also, the rate of extinction can be calculated from $T_e = 1/\lambda$. In the model studied by MacArthur and Wilson (1967), the mean time to extinction increases approximately exponentially with K , the population ceiling for an insular area. Assuming K scales linearly with area, A , we get $\lambda(A) = c \text{Exp}[-bA]$, where c and b are positive constants, which can be inserted into equations 3, 5, and 6 to estimate the effect of fragmentation on extinction risk. This new model predicts either that fragmentation is always detrimental or that it is beneficial in the short term but detrimental in the long term. Fragmentation usually increases the risk of extinction, often drastically, but there exists a small region of parameter space (very small values of bA and c) where fragmentation might reduce the probability of extinction. The median time to extinction also has the property that its derivative with respect to n can be positive for very small values of bA and small values of n . This region may be in biologically unrealistic parameter space, however, and may also be an artifact because the earliest a population can go extinct is after N_0 time steps (Burkey 1995a). Unfortunately, we have no information about the magnitude of b or c . In the vast majority of parameter space, fragmentation increases the probability of extinction and decreases the mean and median time to extinction.

The ecological literature contains two phenomenological models of extinction rates as a function of area. Wilcove et al. (1986) suggests the form

$$\lambda = \frac{e}{\text{Area}}$$

Hanski (1991) proposes that $\lambda = e_0 \text{Exp}[-b \text{Area}]$, which is identical to the model derived above. Like the archipelago data presented here, the model of Wilcove et al. (1986) predicts that fragmentation reduces the probability of extinction in the short term and increases it in the long term. The median time to extinction always decreases with fragmentation in this model.

Conclusion

The procedure I have presented for estimating the effect of habitat fragmentation on the risk of species extinction makes several assumptions that are clearly violated, and much biology is averaged out. In conjunction with other approaches (Burkey 1989, 1993b, 1995a), however, my results support the notion that fragmentation accelerates extinction. As long as fragments are not completely isolated from each other, dispersal between them can alleviate this somewhat—but perhaps not enough to remove the negative effect of fragmentation (see Burkey

1989, 1995a; Forney & Gilpin 1989). On the other hand, dispersal between fragments may also have detrimental effects in fragmented systems, notably by the spread of diseases (see Hess 1994) and by increased mortality for dispersing individuals. Complete isolation of nature reserves from surrounding habitats and from each other must be avoided (see Soulé et al. 1979; Burkey 1995a), reserves should be as large as possible, and the degree of subdivision should be minimized.

Although the assumptions I have made give reason for caution against over-interpretation, most are the same assumptions on which much of the classic theory of island biogeography (MacArthur & Wilson 1967) is based. In light of all the other factors that affect extinction rates, including population size, isolation, elevation, environmental stochasticity, and the number of species present, it is perhaps remarkable that area explains as much of the variation in extinction rates as it does. The effect of fragmentation must be strong indeed to be detected by this procedure despite the many ways in which extinction rates on small islands may be underestimated and despite the diversity of spatial scales represented in the data. Overall, the data sets analyzed here yield a strong indictment of anthropogenic habitat loss and fragmentation as a severe threat to global biodiversity. Sadly, there are numerous reasons why my estimates of how fragmentation accelerates the loss of species may be conservative.

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Patch Isolation, Corridor Effects, and Colonization by a Resident Sparrow in a Managed Pine Woodland

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Abstract: The isolation of habitat patches is often cited as having a major impact on the dynamics of small populations occupying patches in a complex landscape. Few studies, however, have provided field data demonstrating that isolation has an identifiable effect on specific populations independent of other factors such as local habitat quality or that landscape factors such as corridors can alleviate such effects. We conducted field surveys of Bachman's Sparrow (*Aimophila aestivalis*) populations in regions, which we call linear landscapes, where suitable habitat patches were isolated to varying degrees from potential sources of dispersing birds. In these linear landscapes, isolated patches of habitat were less likely to be colonized than were nonisolated patches. We also found that corridor configurations of habitat patches improved the ability of sparrows to find and settle in newly created patches. These results suggest that, for species that do not disperse easily through inhospitable landscapes, habitat occupancy at a regional scale can be enhanced by careful landscape design and planning.

Aislamiento de parches, efecto de los corredores y colonización de un gorrión residente en un Pinar bajo manejo

Resumen: El aislamiento de los parches de hábitat, es a menudo citado como un factor que tiene un gran impacto sobre la dinámica de poblaciones pequeñas, que ocupan parches en paisajes complejos. Sin embargo, muy pocos estudios han brindado datos de campo que demuestren que el aislamiento tiene un efecto reconocible sobre poblaciones específicas, independientemente de factores tales como la calidad del hábitat, u otros factores tales como los corredores que pueden aliviar tales efectos. Conducimos estudios de campo de poblaciones del gorrión de Bachman (*Aimophila aestivalis*), en regiones que nosotros llamamos "paisajes lineales"; donde los parches de hábitats estaban aislados, en distinto grado, de potenciales fuentes dispersoras de pájaros. En estos paisajes lineales los parches de hábitats aislados eran menos proclives a ser colonizados que los parches no-aislados. También encontramos que las configuraciones en corredor de los parches de hábitats mejoró la habilidad de los gorriones para encontrar y establecerse en parches creados recientemente. Estos resultados sugieren que para aquellas especies que no se dispersan fácilmente a través de paisajes inhospitarios, la ocupación del hábitat a escala regional puede ser mejorada mediante un cuidadoso diseño y planificación del paisaje.

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